



Birds in boreal protected areas shift northwards in the warming climate but show different rates of population decline

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ABSTRACT

Climate change has the potential to have wholesale impacts on species populations, driving them polewards and upwards, and even affecting populations occurring within protected area (PA) networks. We studied population changes in bird species in the boreal PA network of Finland based on extensive bird census data collected in the years 1981–1999 and in 2000–2017. Between these time periods, the mean annual temperature increased in Finland by 1.1 °C, and the mean weighted density of the species shifted 28.5 km (1.8 km/year) northwards in the PA network. However, the total bird population density simultaneously declined by approximately 10%. The decline was most pronounced in long-distance migrants, which showed strongest population contraction in southern boreal regions. In contrast, resident species increased between the two time slices, particularly in larger PAs. While the PA network of boreal native habitats appears to be successful in preserving resident species, climate-induced changes have also caused a decline in the populations of migrants in the PAs. Thus, life-history characteristics of species can significantly affect the success of conservation efforts in a warming climate. To enhance future survival of resident and migrant bird species moving to Finland and northwards, the PAs should be larger and the connectivity of the PA network improved in southern and central Finland. In addition, international actions are needed to enhance the survival of long-distance migrants during the migratory period and in overwintering grounds.

1. Introduction

A key aim of the protected area (PA) network is to ensure the maintenance of populations, species and communities, but there are several challenges in reaching this target (Rodrigues et al., 2004; Gaston et al., 2008). Importantly, ongoing climate change is putting accelerating pressure on species to move polewards and upwards (Parmesan, 2006; Huntley et al., 2007, 2008; Pereira et al., 2010; García et al., 2014), which, in turn, is creating further demands for the PA network to efficiently preserve biota (Hannah et al., 2007; Araújo et al., 2011). In extreme cases, PA networks may cease to afford protection to those species for which they were originally established (Coetzee et al., 2009; Hole et al., 2009), but the evidence for such prospects is mixed, and a number of recent studies have actually shown that well-established effective PA network can provide important support for species movements to, and population establishment in, new areas, even under changing climatic conditions (Thomas et al., 2012; Gillingham et al., 2015). PA networks may also alleviate, at least

temporarily, the negative effects of climate change on species and communities (Virkkala et al., 2014; Gaüzère et al., 2016; Santangeli et al., 2017).

In addition to changes in species distributions, their abundances are also moving polewards (Virkkala and Lehikoinen, 2014; Lehikoinen and Virkkala, 2016). The latitudinal density shift of species may affect community composition (see, e.g. Lindström et al., 2013). However, the challenge here is that density shifts are not as easily observable as species range shifts. This is because, to be discovered, they require quantitative censuses of species over wide areas. Densities of species with large distribution areas may also shift latitudinally to a considerable degree without any observable change in their range limits. Because of these methodological challenges, it is highly important to know how the population densities of species have changed in the PA network under a changing climate, and most importantly, if they exhibit hidden decreasing density trends in PAs that are not apparent in species presence-absence monitoring data or in country-wide population density monitoring data.

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Examining species density changes in the PAs of northern boreal and Arctic regions is a particularly important task. This is because the Arctic Ocean represents an effective natural barrier to species' northward range shifts (Virkkala et al., 2008). In addition, for our study area, Finland, the Baltic Sea creates a barrier for the northward movement of southern species and for recruits from more southern regions. Moreover, climate-change-driven changes in biota are projected to be most dramatic at northern latitudes because of the greater temperature increase in these regions (Jetz et al., 2007). For example, in Finland the ratio of the annual mean temperature increase to the global mean increase is projected to range from 1.6 to 1.9 depending on the greenhouse gas scenario, and the annual mean surface air temperature will increase by 2 to 5.5 °C by 2080 in comparison with the baseline period, 1981–2010, depending on the scenario (Ruosteenoja et al., 2016). Annual mean temperatures in Finland increased by 0.7 °C in the years 1901–2000, with most of the increase occurring at the end of the century (see Jylhä et al., 2004).

In northern Europe, the boreal landscape has been intensively utilized; in particular, forestry together with agriculture account for the major land use in vast areas. In Finland, both mires and old-growth forests, in particular, are focal habitats for the conservation of biodiversity, and specific protection programmes for both of these habitats have been implemented (OECD, 1997; Auvinen et al., 2010). Approximately 12% of all mires and > 7% of forest land with over half of all remaining old-growth forests have been protected. Such PAs may thus provide important sites for species conservation. However, great geographic differences exist in the cover of PAs, as, i.e. approximately 80% of the protected land is situated in northern Finland (Virkkala et al., 2000), where the protected area network thus is the largest and the most representative.

With birds, migratory habits create a further complicating factor in studying climate-change-driven effects on species. This is because in the northern, boreal latitudes, some breeding bird species overwinter in tropical areas either in Africa or in Asia, some in temperate or Mediterranean areas, while with some species part of the population is migratory and part is resident (partial migrants). Additionally, certain species are true residents. These different migratory groups may face quite different environmental variations in their life cycle. For example, spring temperatures greatly affect the arrival of migrants (Saino et al., 2011), and mild winters may enhance the survival of residents and partial migrants (Lehikoinen et al., 2016). However, relatively little is known about how the densities of birds representing different migratory habits have changed in the protected areas and whether there are notable differences between the species groups that might be reflected in the persistence of species.

In our study, we compared population changes of birds from the years 1981–1999 to 2000–2017 in the PA network in Finland extending 1100 km across the boreal zone (Fig. 1). Between these time slices, a clear warming of the climate had already occurred. Our study is based on large-scale bird inventories (almost 20,000 transect km) carried out in 254 PAs with a total area of almost 28,000 km². We examined the following questions: (1) How do the temporal population changes differ in the PA network between the different migratory groups and how well does the PA network maintain populations in a warming climate? (2) Are there different patterns in population changes along the latitudinal gradient? (3) Are there patterns of latitudinal density shifts of species in the PA network, and are they different between different species groups?

2. Material and methods

2.1. Protected areas

Finland stretches 1100 km across the boreal biome of northern Europe (Fig. 1). The PA network in Finland is largely concentrated in the north and is mostly covered with coniferous (dominated by Scots

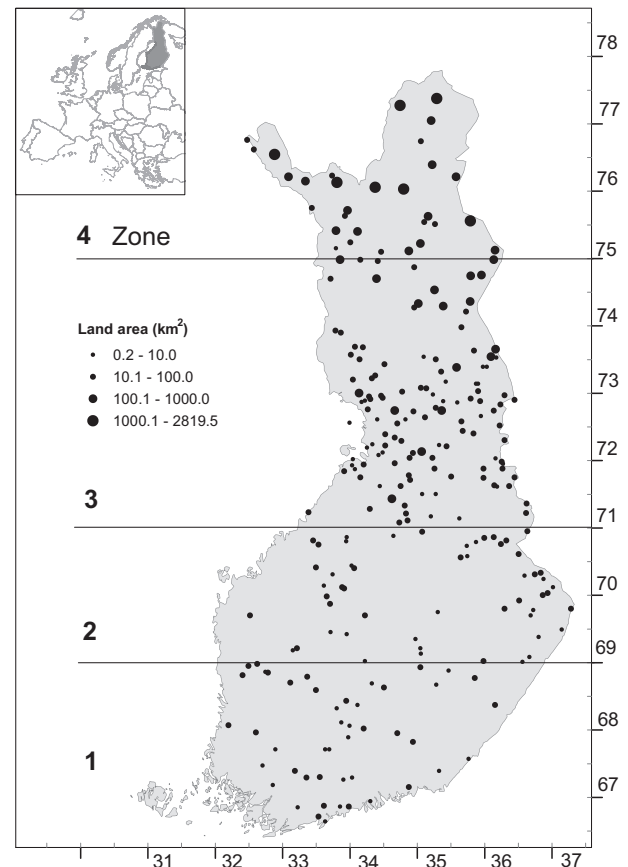


Fig. 1. Location of protected areas studied. Zones 1–4 from south to north are presented. Grid numbers are from the Uniform Coordinate Systems (uniform grids) used in Finland.

pine *Pinus sylvestris* or Norway spruce *Picea abies*), mixed and deciduous (dominated mainly by birch *Betula* spp) forests, open mires (treeless peatlands), marshlands, and Arctic mountain heaths.

Birds were counted both in 1981–1999 and in 2000–2017 in 254 PAs. In these PAs the total land area was 27,851.6 km², constituting approximately 70% of total land area of all PAs in Finland (Fig. 1, Fig. A.1). The median size of studied PAs was 20.7 km², with a size range between 0.2 and 2819.5 km². Five areas were smaller than 1.0 km² and four areas larger than 2000 km², and all of the largest PAs are situated in northernmost Finland (Fig. 1). In order to examine the potential large-scale geographic differences in the bird population density changes, we divided the country into four regions (zones) from south to north (see Fig. 1), and the median sizes and number of studied PAs in these zones (1–4) were as follows, respectively: 10.1 km² (N = 44), 12.1 km² (N = 54), 19.5 km² (N = 110) and 132.9 km² (N = 46).

Logging or drainage of mires is prohibited in the protected areas, so forestry is not allowed in these areas. Forests (including wooded mires) cover 56% of the land in the studied reserves, with the rest being open, treeless mires and mountain areas. In the southern half of Finland, forests cover 70% of the land area in the PAs, while in the northern half they cover 54% of the land area in the PAs. More than two thirds of the protected forest stands are over 100 years old (Virkkala et al., 2000).

2.2. Bird censuses

Land birds in protected areas were counted by using the Finnish line transect census method (Järvinen and Väisänen, 1976), which is suitable for counting birds over large areas (Väisänen et al., 1998; Virkkala and Lehikoinen, 2014). The line transect method applies a one-visit census in which birds are counted during breeding season along a

transect with an average length of 5–6 km.

The census was carried out in late May and in June in the early morning, when the singing activity of birds was at its peak. In the line transect census, a 50-metre-wide main belt along the walking line (25 m on each side) and a supplementary belt outside the main belt are separated. The latter covers all land birds observed outside the main belt (e.g. Järvinen and Väisänen, 1976; Järvinen et al., 1991; Väisänen et al., 1998). In the Finnish line transect, the densities of species based on the observations in the censuses are calculated in standard units of pairs/km². A pair was inferred from a male heard singing, from an otherwise observed male or female, or from a group of fledglings according to the instructions for the Finnish line transect census (for details, see Järvinen and Väisänen, 1976; Järvinen et al., 1991).

Densities of bird species (pairs/km²) were calculated on the basis of observations in the whole survey belt, including both the main and supplementary belts. As a baseline rule, the density of a species (D , pairs/km²) was calculated as follows:

$$D = K \times N/L, \quad (1)$$

where K = species-specific correction coefficient, N = number of observations of a species in the whole survey belt and L = transect length (in km). Species-specific correction coefficients (K) were used in the density calculations to correct for the differences in the detectability of species, calculated as follows (Järvinen and Väisänen, 1983):

$$K = 40 - 40\sqrt{1-p}, \quad (2)$$

where p = proportion of main belt observations (range 0–1); for more detail on the calculations, see Järvinen and Väisänen (1983). These coefficients vary according to the proportion of main belt observations to all survey belt observations.

The species-specific correction coefficient takes into account the differing audibility and other detectability of different species (Järvinen and Väisänen, 1983). The value of this coefficient is low for a species for which only a small proportion of all observations come from the main belt (e.g. common cuckoo *Cuculus canorus*). By contrast, the coefficient's value is high for species for which a large proportion of the observations are made in the main belt (e.g. western capercaillie *Tetrao urongallus*). In addition, the detectability of a species may change during the breeding season, such as in the case of the black grouse *Lyrurus tetrix*, for which the lekking period with singing (lekking) males usually ends by mid-June (see Table A.1). All species-specific correction coefficients used in this study were calculated on the basis of line transect data collected from protected areas in Finland and neighbouring countries (see Table A.1).

The total length of line transect censuses in the protected areas was 9102 km in 1981–1999 and 10,424 km in 2000–2017. Birds were counted in 254 areas, for which the total length of the transects during both periods was at least 1.0 km (see Fig. 1). The mean total length of the transects in a PA was 35.8 km in 1981–1999 and 41.0 km in 2000–2009. The median number of years when censuses were carried out in each protected area was two both in 1981–1999 and in 2000–2017. The median census year was 1994 in the first period and 2010 in the second period, making the average time span in the study 16 years. The same exact transects were not repeated, but censuses in each protected area included the same proportion of habitats during the two periods.

2.3. Statistical analyses

Bird species were classified according to their migratory status: (1) long-distance migrants, (2) short-distance migrants, (3) partial migrants and (4) residents (Väisänen et al., 1998; Laaksonen and Lehikoinen, 2013; Lehikoinen and Virkkala, 2016; Virkkala and Lehikoinen, 2017; see Table A.1). Short-distance migrants include species wintering in central and southern Europe and in the Mediterranean region. Long-distance migrants overwinter in Africa south of the Sahara or in

southern or southeastern Asia.

We compared geographic differences in the population density changes of species in the PA network by dividing Finland into four latitudinal zones from south to north (Fig. 1). We used two-factor ANOVA in which geographical location (zone), temporal change (from 1981 to 1999 to 2000–2017) and their interaction were considered (Quinn and Keough, 2002). In studying total bird density and long-distance and short-distance migrants, the original density values were log-transformed. In the case of partial migrants and residents, the density values were square root –transformed, because the density values in some areas were zero or below one. For the most abundant species, a rank-order ANOVA was applied (Thomas et al., 1999) in the species-specific comparisons because of a highly skewed non-normal distribution of density variation with a high proportion of zero values in the data. Density changes in the eight most abundant bird species were investigated in more detail, six of which were forest-dwelling species (common chaffinch *Fringilla coelebs*, willow warbler *Phylloscopus trochilus*, brambling *Fringilla montifringilla*, spotted flycatcher *Muscicapa striata*, tree pipit *Anthus trivialis*, and Eurasian siskin *Carduelis spinus*) and two breed in open mires and in Arctic mountain heaths (meadow pipit *Anthus pratensis* and yellow wagtail *Motacilla flava*). For other comparisons of changes in species density changes between the time slices, a non-parametric Wilcoxon signed rank –test was applied.

The mean weighted latitudinal and longitudinal density shifts (in km, based on uniform grid) in the PA network from 1981 to 1999 to 2000–2017 was calculated for all species observed in at least 25 PAs (in 10% of all PAs). The effect of the size and location (latitude) of a PA on the density change in different bird species groups was studied using linear regression analyses. The log-transformed size of PAs was included in the regression analyses so as to take into account the impact of varying PA sizes. Although the largest PAs were situated in northernmost Finland, the correlation between latitude and the size of all PAs was only moderate ($r = 0.55$, $p < 0.001$, $N = 254$).

Density change in each PA was measured as a log ratio of per cent change in density. Percentage changes above and below 100% are not strictly comparable; for example, a doubling increase from 100 gives a value of 200, but a similar decrease to half that yields 50. To avoid this discrepancy, we used the logarithmic ratio (log ratio) of per cent change in densities, where, for example, a 100% increase in density from 1981 to 1999 to 2000–2017 would be $\log(200/100) = +0.301$ and a 50% decrease would be $\log(50/100) = -0.301$.

2.4. Climate data

We compared the trends in two climate variables known to be among the main climatic drivers affecting bird species distributions (e.g. Heikkinen et al., 2006; Huntley et al., 2007): the mean annual temperature (T_{Ann}) and the mean April–June temperature of (T_{AMJ}). T_{AMJ} particularly affects the arrival and breeding of the migratory birds, whereas T_{Ann} affects residents and partial migrants. The data for these climate variables were based on 10×10 km gridded data covering all of Finland and were obtained from the Finnish Meteorological Institute (Tietäväinen et al., 2010). For the comparisons, we included the values of the climate variables recorded for the study years in the four zones

Table 1

Mean April–June (T_{AMJ}) and annual temperatures (T_{Ann} , °C) in Finland in the study zones 1–4 in 1981–1999 and in 2000–2017.

Zone	T_{AMJ}		T_{Ann}	
	1981–1999	2000–2017	1981–1999	2000–2017
1	8.18	9.08	4.25	5.36
2	7.40	8.33	2.68	3.78
3	5.72	6.73	0.67	1.79
4	3.08	4.28	-1.51	-0.38

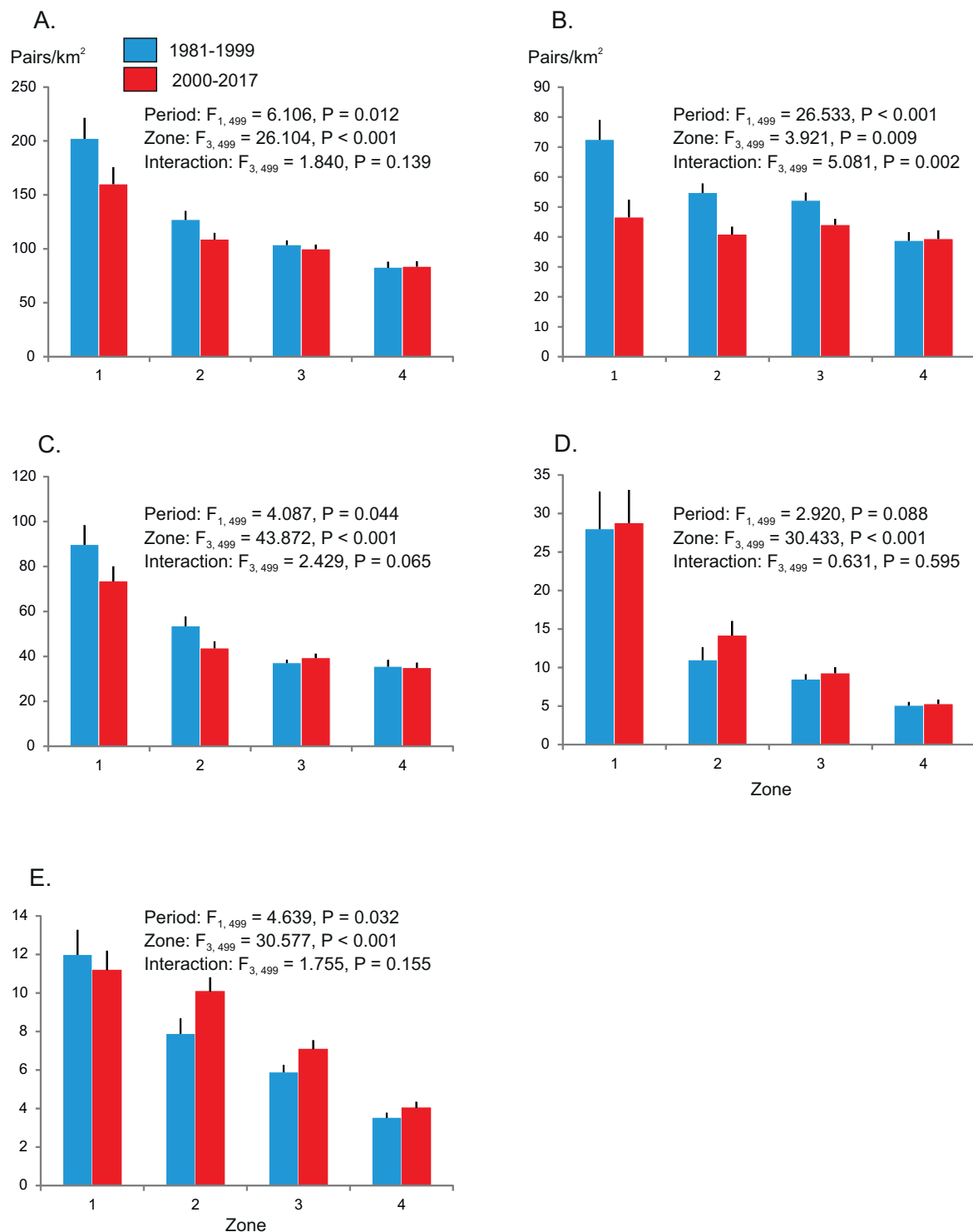


Fig. 2. Mean \pm standard error (S. E.) in density of birds (pairs/km²) in the protected areas in zones 1–4 in the two periods, with results of the two-factor ANOVA (Period, Zone and their Interaction). A = total bird density, B = long-distance migrants, C = short-distance migrants, D = partial migrants and E = residents.

(Table 1). The mean annual temperature increased by 1.1 °C and the mean April–June temperature by 1 °C between the study periods, on average. Geographic shifts due to global warming can be observed, for example, in the T_{AMJ}, in which the value in 2000–2017 was already higher in zone 2 than it was in 1981–1999 in the more southern zone 1 (Table 1).

3. Results

Total bird density (pairs/km²) in the PA network declined by 10.5% between 1981 and 1999 and 2000–2017 (mean \pm S.E.; 1981–1999: 122.1 ± 4.7 p/km², 2000–2017: 109.3 ± 3.7 p/km²). Interestingly, total bird density declined particularly in the PAs situated in southern Finland (zones 1 and 2), but not in northernmost Finland (zone 4, Fig. 2). When comparing two zones with similar climatic conditions in the two time slices (i.e. zone 1 in 1981–1999, 202.3 ± 18.7 p/km²,

and zone 2 in 2000–2017, 108.9 ± 5.5 p/km²; see Table 1) in southern Finland, it became clear that the total bird density had declined by almost half.

When species were divided according to their migratory habits, different patterns emerged. Long-distance migrants declined considerably, by about 20% (1981–1999: 53.8 ± 1.8 p/km², 2000–2017: 43.0 ± 1.4 p/km²). This decline was the most pronounced in the PAs in southernmost Finland (zone 1), and the difference between the densities in 1981–1999 and 2000–2017 levelled off further north (Fig. 2 and Fig. 3). Similar patterns emerged for short-distance migrants, but residents, in contrast, increased somewhat between the time slices (1981–1999: 11.8 ± 1.0 p/km², 2000–2017: 13.0 ± 1.0 p/km², Fig. 2). Residents include, in particular, gallinaceous species, woodpeckers and tits. Typical resident species preferring old-growth forests or a continuous forest landscape either remained stable (Siberian tit *Poecile cinctus*, Wilcoxon signed rank, $z = 1.144$, $P = 0.253$, $N = 254$; Siberian jay *Perisoreus infaustus*, $z = 0.788$, $P = 0.431$) or even increased (three-toed woodpecker *Picoides tridactylus*, $z = 5.509$, $P < 0.001$; western capercaillie, $z = 2.722$, $P = 0.006$; for densities, see Table A.1). Furthermore, declining resident willow tit *Poecile montanus* remained stable ($z = 0.239$, $P = 0.831$) and crested tit *Lophophanes cristatus* even increased ($z = 3.121$, $P = 0.002$) in the PAs (see Table A.1).

When studying the effects of latitude and the size of a PA on the observed density change, latitude proved to be significantly related to the density change in long-distance migrants, short-distance migrants and partial migrants (Table 2, Fig. 3). In contrast, the size of a PA was positively related to the density change in residents (Table 2).

At the species level, six of the eight most abundant species declined, one species increased (Eurasian siskin) and one species (spotted flycatcher) did not show a significant change between the study periods (Fig. 4, Table 3). In five of the six declining species, there was interaction between the period and the location (zone) of the PA, indicating that the patterns were different in the different parts of the country. All of the declining species decreased most in the southernmost regions (zones 1–2) and least in the northernmost region (Fig. 4).

The mean weighted latitudinal density (MWLD) shift of species was,

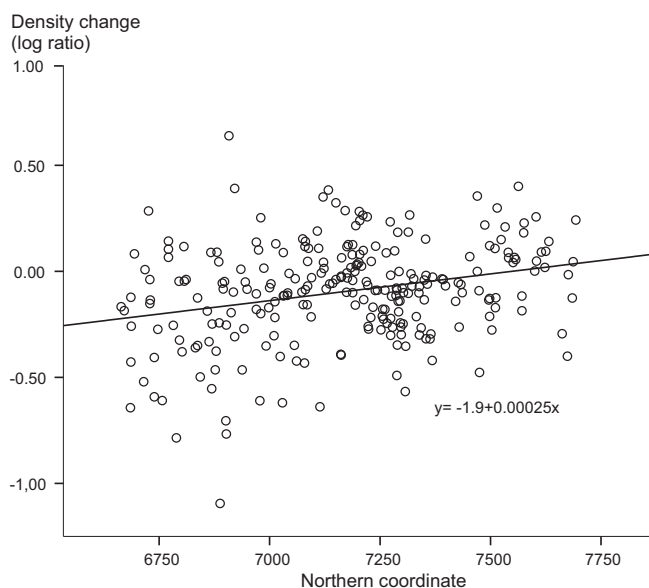


Fig. 3. Density change (log ratio) of long-distance migrants in each protected area in relation to location (latitude). Per cent change in density is based on log ratio, where, for example, 100% increase in density from 1981 to 1999 to 2000–2017 is $(200/100) = +0.301$ and 50% decrease is $\log(50/100) = -0.301$. Northern coordinate is according to uniform grid (distance from the equator).

Table 2

Linear regression of change in bird density between 1981 and 1999 and 2000–2017 based on log ratio $[(\log(\text{density in 2000–2017}/\text{density in 1981–1999}))]$ in each protected area (PA) with latitude (northern coordinate) and size of each PA as explanatory variables.

Migratory group	Regression			Coefficients			
				Latitude		Size	
	F	df	P	t	P	t	P
Long-distance migrants	9.999	2, 251	< 0.001	3.814	< 0.001	0.160	0.873
Short-distance migrants	3.409	2251	0.035	2.212	0.028	0.065	0.948
Partial migrants	2.345	2, 247	0.098	2.163	0.032	1.100	0.273
Residents	2.118	2, 245	0.122	0.847	0.398	2.030	0.043

on average, 28.5 ± 5.9 km northwards in the PA network ($N = 105$, 1.8 km/year; see Table A.1). The MWLD shift did not differ significantly between the migratory groups (Kruskal-Wallis test, $df = 3$, $\chi^2 = 2.225$, $P = 0.527$), being, on average, 34.6 ± 12.1 km northwards in long-distance migrants ($N = 38$), 28.2 ± 8.1 km in short-distance migrants ($N = 35$), 28.0 ± 16.4 in partial migrants ($N = 17$) and 14.0 ± 10.0 km northwards in residents ($N = 15$). The MWLD shifted, on average, 52.3 km (range 28.4–87.2 km) northwards for the eight most abundant species (Table 3).

The mean weighted longitudinal density shift of species was, on average, only 4.4 ± 2.4 km westwards ($N = 105$; see Table A.1), and there was no difference in this shift between the migratory groups (Kruskal-Wallis test, $df = 3$, $\chi^2 = 5.210$, $P = 0.157$).

4. Discussion

We showed that total land bird population densities in the PAs have decreased due to the decline of migrants, particularly long-distance migrants. Long-distance migrants have been observed to be declining both in Europe in general (Sanderson et al., 2006; Gregory et al., 2007; Vickery et al., 2014) and in Finland (Laaksonen and Lehtikoinen, 2013), where the ranges of long-distance migrants have also contracted (Virkkala and Lehtikoinen, 2017). However, most previous studies have employed abundance and distribution data mainly from areas outside the PA network (see, however, Johnston et al., 2013; Amano et al., 2018), exposing them to the confounding impacts stemming from multiple drivers. In contrast, using the PAs as the focal study areas enabled us to exclude the direct effects of local and regional drivers, such as land use, on the revealed temporal changes in the population densities of species. Among the observed density trends in the PA network, one of the most notable points is that migrants have decreased in PAs situated in southern Finland but not in northernmost Finland. Intriguingly, the largest PAs are situated in northernmost Finland, but there was no positive correlation between size and density change either in the long-distance or in the short-distance migrants. In contrast, latitudinal location was related positively to the change in density in both of these migratory groups.

These findings beg the question of why migrants have declined in southern Finnish PAs but not in northernmost PAs. One factor might be the prolonged migration of migrants in springtime (Berthold, 2001). In warmer springs, migrants fly further north than in colder springs. This prolonged migration probably affects especially juveniles, first breeders, which are not site tenacious but disperse from their natal breeding area. Thus, although the populations might have declined equally both in southern and northern PAs, it is possible that the first breeder recruits from the south have compensated for the losses in the north. This is linked with trends in spring temperatures. In particular, April mean temperatures, which are highly important for migratory species (see, e.g. Sainio et al., 2011) have clearly risen in Finland (Ruosteenoja et al.,

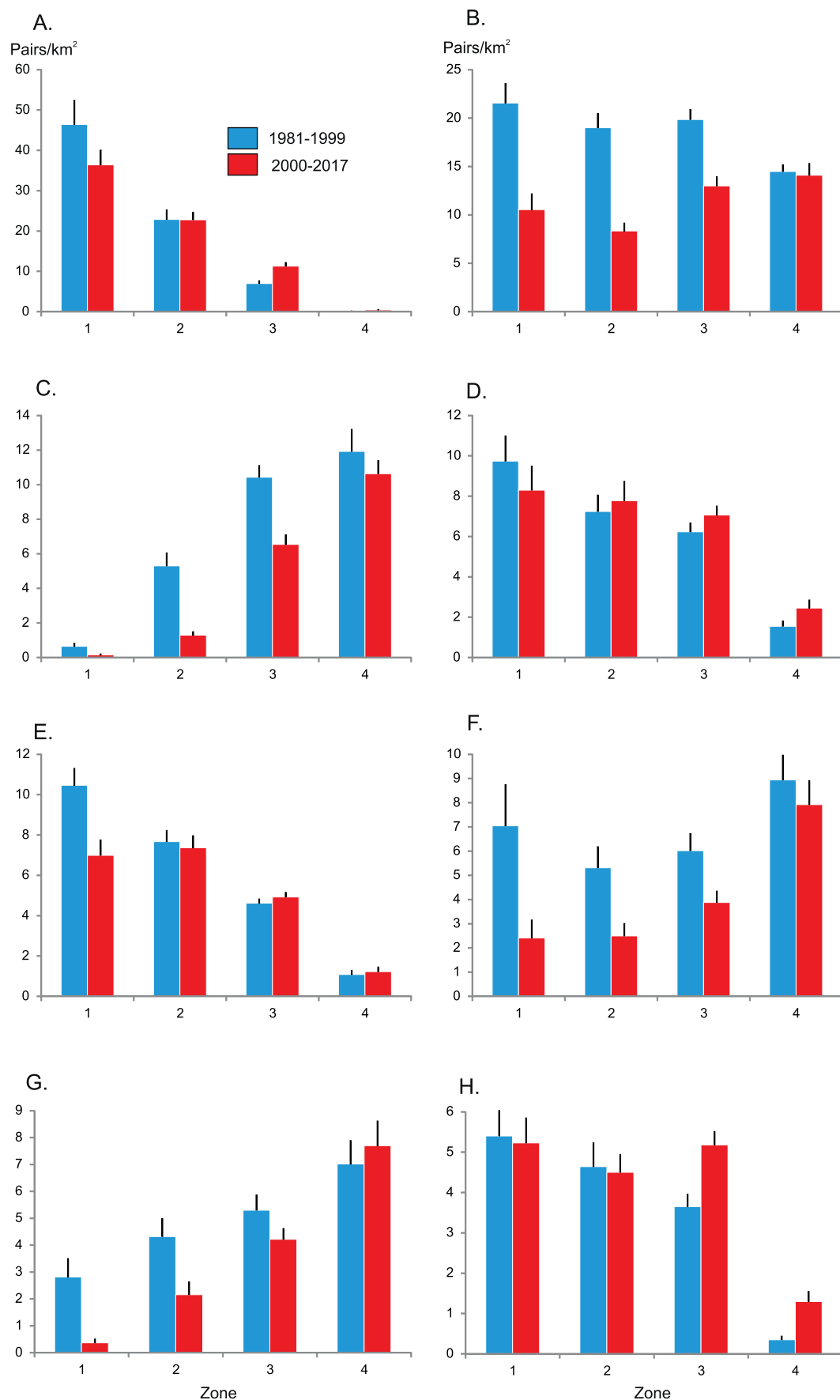


Fig. 4. Mean \pm S. E. in density of the eight most abundant bird species (pairs/km²) in the protected areas in zones 1–4 in the two periods. A = common chaffinch *Fringilla coelebs*, B = willow warbler *Phylloscopus trochilus*, C = brambling *Fringilla montifringilla*, D = spotted flycatcher *Muscicapa striata*, E = tree pipit *Anthus trivialis*, F = meadow pipit *Anthus pratensis*, G = yellow wagtail *Motacilla flava*, and H = Eurasian siskin *Carduelis spinus*.

Table 3

Significance of population changes of eight most abundant bird species based on two-factor ANOVA with time period (df = 1, 499) and zone (df = 3, 499) as the main factors. Interaction of factors is shown (df = 3, 499), and the size of the protected area (log-transformed) was a covariate in the analyses. Mean weighted northward shift in density between 1981 and 1999 and 2000–2017 is presented (in km). L = long-distance migrant, S = short-distance migrant.

Species	Period		Zone		Interaction		Shift (km)
	F	P	F	P	F	P	
<i>Fringilla coelebs</i> (S)	7.09	< 0.001	175.79	< 0.001	4.03	0.008	+55.7
<i>Phylloscopus trochilus</i> (L)	77.68	< 0.001	2.80	0.040	7.11	< 0.001	+54.3
<i>Fringilla montifringilla</i> (S)	29.13	< 0.001	107.59	< 0.001	5.83	0.001	+51.5
<i>Muscicapa striata</i> (L)	1.24	0.266	39.66	< 0.001	0.91	0.436	+28.4
<i>Anthus trivialis</i> (L)	4.77	0.029	92.09	< 0.001	5.63	0.001	+32.5
<i>Anthus pratensis</i> (S)	12.30	< 0.001	5.48	0.001	0.67	0.57	+87.2
<i>Motacilla flava</i> (L)	11.51	0.001	19.55	< 0.001	4.09	0.007	+55.2
<i>Carduelis spinus</i> (S)	10.21	0.002	33.99	< 0.001	2.17	0.090	+53.4

2016); thus the warming of springs has provided increased possibilities for the northwards movement of migratory birds. In contrast, adults in many boreal migratory species are site tenacious and return to their earlier breeding sites (e.g. the willow warbler (Tiainen, 1983) and the chaffinch (Mikkonen, 1983)). Moreover, it seems that the PAs in southern Finland do not receive recruits from the more southern regions, i.e. areas south of the Gulf of Finland, or else they receive too few recruits to compensate for birds moving further north. This decline in bird populations may be related to the fact that the Baltic Sea can restrict the movement of migrants north.

Another potential driver for the migrant decline is food availability, which can affect species survival at several points of their lifecycle, including the time spent at the stop-over sites during the spring migration. Hallmann et al. (2017) recently showed that the total biomass of flying insects in German protected areas had declined by 76% in a period of 27 years. These protected areas are situated in forests, but surrounded by agricultural areas. Many Finnish short-distance migrants overwinter in Central Europe, and moreover, long-distance migrants wintering in Africa may use these habitats as stop-over sites during migratory periods. Long-distance migrants are insectivorous, while short-distance migrants are either insectivorous or else prefer foraging on insects in spring and summer. Thus, the biomass losses of Central European insects may have cascading effects, with one manifestation of such effects being the decline of migrants in northern European protected areas due to the loss of food resources during wintering and migratory periods. Further potential support for this hypothesis comes from Britain, where insects, i.e. moths, have shown corresponding declining trends (Fox et al., 2014). There is no data on changes in total insect biomass from the bird breeding grounds in Finland. However, total moth abundances in Finland exhibited no clear decline during the period 1993–2012 (Leinonen et al., 2016), suggesting that factors inducing declines in the densities of long-distance and short-distance migrants occur in overwintering areas or in stop-over sites during migration.

Our results show that an overall shift is also occurring in the species densities of bird populations in the boreal PA network, causing them to shift northwards. In contrast with species latitudinal density shift, longitudinal shift in density of species was very small showing that northwards climate warming is probably the primary driver of species density shifts. The velocity of the latitudinal density shift of the studied bird species (1.8 km/year) is about the same as in studies carried out in the whole country, meaning, on average, 1.5 km/year in 128 species between the time periods 1970–1989 and 2000–2012 (Lehikoinen and Virkkala, 2016). However, in the most abundant species in the PA network, the density shift was even higher, over 3 km/year. Thus, climate-induced northward density shifts are clearly observable also in the PAs. Interestingly, Välimäki et al. (2016) observed that the velocity of density shift was higher in partial migrants and residents than in short- and long-distance migrants in a study carried out in the whole of Finland. They suggested that this was due to warmer winters combined

with increased food provisioning by humans, thus allowing residents and non-migrating partial migrants to survive better at higher latitudes and causing the northward density shifts of these groups. In the PAs, we observed no significant change in the velocity of the northward shift between the migratory groups, probably due to the fact that direct human-caused factors are not as strongly reflected in bird populations in the PAs as outside of them.

Recent findings suggest that PAs may alleviate the negative effects of climate change because PAs have maintained higher richness of species of conservation concern than areas outside PAs. Such a trend became evident when comparing bird species richness patterns between 1974 and 1989 and 2006–2010, a period with notable warming of climate in Finland (Virkkala et al., 2014). Another study showed that the community temperature index (CTI) measuring the relative temperature average of a community of bird species assemblage has remained higher in Finnish PAs than outside PAs from 1970 to 1989 to 2000–2014 (Santangeli et al., 2017). Importantly, CTI was higher in PAs due to higher proportion of northern, cold-adapted species therein, suggesting that PAs may indeed slow down the decline of northern species in their contracting range margin (Santangeli et al., 2017).

Many migratory birds, such as the chaffinch, willow warbler, redwing *Turdus iliacus*, tree pipit, rustic bunting *Emberiza rustica* and scarlet rosefinch *Carpodacus erythrinus*, have also declined in managed forest landscape outside PAs (Laaksonen and Lehikoinen, 2013; Fraixedas et al., 2015; Virkkala, 2016). Some species, such as the willow warbler and redwing actually prefer logged and fragmented forests and young successional stages (Helle and Järvinen, 1986; Virkkala, 1987, 1991) and they might therefore be expected to increase due to intensive forestry with clear-cutting and resulting young stands. Therefore, their decline in PAs cannot be due to the negative effects of logging outside the PAs (see Häkkinen et al., 2017). These species have declined both in PAs and in areas outside PAs showing the overall effect of climate change. However, forest succession in the PAs may affect their density.

Northern species, such as brambling, yellow wagtail and meadow pipit, seem to have declined quite dramatically, particularly in the southern PAs, where the population densities of these species decreased to clearly less than half during the study period. Northern species decreased most in their southern, trailing edge, while southern species (e.g. Eurasian Siskin) increased most in their northern, leading edge (Virkkala and Rajasärkkä, 2011). The decline of northern species is also in line with climate change predictions (Virkkala et al., 2008, 2013) and has also been observed throughout the country (Laaksonen and Lehikoinen, 2013).

In contrast with the decline of migrants, the populations of partial migrants have not changed, and residents have even increased, on average, in the PAs. This pattern is strikingly different from that of migratory species. For residents, latitude did not affect the observed trend, but the size of a PA was positively related to the population change. Already Virkkala (1987, 1991) observed that the populations of

resident northern taiga species (western capercaillie, three-toed woodpecker, Siberian tit, Siberian jay) remained stable in large virgin forest tracts but declined in logged and fragmented forest landscapes in a period from the 1940s–1950s to the 1980s. The implementation of old-growth forest and other protection programmes has clearly been successful for the protection of these resident species, which declined considerably between the 1950s and the late 1970s (Järvinen and Väisänen, 1979; Lindén and Rajala, 1981). Part of the newly protected forests have previously been managed by forestry practices, particularly in southern Finland, and the volume of dead wood is now increasing in these areas due to natural disturbances (e.g. wind falls and an increase in standing dead trees) or restoration activities benefitting species that require dead wood, e.g. woodpeckers, such as the three-toed woodpecker. Moreover, resident willow tit and crested tit have considerably declined in Finland during the past decades due to logging practices (Siffczyk et al., 2003; Virkkala, 2004; Eggers and Low, 2014), and these species are now regarded even as threatened (vulnerable; Tiainen et al., 2016). However, in the whole PA network willow tit and crested tit have not declined showing that for the resident species the patterns of population changes are different in the PAs and in areas outside them.

In the boreal biome, the total bird density increases towards the south, and this density in a given habitat is much higher in the southern transitional hemiboreal zone and in the temperate biome in more southern regions (see Järvinen and Väisänen, 1980; Väisänen et al., 1998; Wesolowski et al., 2006). This southward increase can also be observed in the present PA network, with a significant difference in density between PAs in the different latitudinal zones. However, total population density declined in spite of the warming climate, and under similar climatic conditions between 1981 and 1999 (zone 1) and 2000–2017 (zone 2) in southern Finland even quite drastically. Thus species, particularly migrants, in the PA network are not able to track climate change possibly due to dispersal barriers and a lag of time of species response to global warming (Devictor et al., 2008; Devictor et al., 2012; Lehtikoinen and Virkkala, 2016).

Finally and perhaps not surprisingly, our results are parallel with the predictions of species occurrences for the 21st century. Based on bioclimatic envelope modelling, the occurrences of species of conservation concern are predicted to shift considerably towards the north in Finland both in protected and in unprotected areas by 2051–2080 (Virkkala et al., 2013). The occurrences of forest birds are predicted to decrease most in southern Finland because the potential gain of expanding southern species of conservation concern (occurring presently south of Finland) will apparently not compensate for the loss of the present boreal species in southern parts of the country (Virkkala et al., 2013).

5. Conclusions

This study shows that life-history characteristics of species may considerably affect the success of species conservation in a warming climate (see Pöyry et al., 2009).

The dispersal abilities of bird species are, in general, fairly good in relation to many other species groups, and the good dispersal ability of individual birds enables shifts in species range. Conservation efforts, such as establishing protected areas of boreal native habitats (e.g. old-growth forests, open mires, alpine heaths), have been successful in preserving resident bird species, but they do not seem to be able to prevent the climate-induced decline of migrants in the boreal protected area network. However, the size of PAs had a positive effect on the trends of residents, which means that larger areas should be protected and the connectivity of the PA network enhanced, particularly in southern and central Finland, to ensure the possibilities for the northward shift of residents, many of which are threatened by forestry outside PAs. For migrants, further studies are needed to pinpoint the factors affecting their decline (see Both et al., 2010; Vickery et al., 2014). It would be especially interesting to verify whether or not the declining

insect biomass in Central Europe has affected migratory birds' survival during their migration or wintering periods. Quick action is needed, as the rapidly warming climate will probably cause further, accelerating declines of bird populations in the presently boreal biome during this century, when the centres of gravity of species abundances approach the coast of the Arctic Ocean.

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